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Gaps in Darwin's Initial Theory



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Synonyms

[Criticisms of Darwin's work on natural selection](#); [Shortcomings in the *Origin of Species* related to Darwin's/Wallace's theory of natural selection](#)

Definition

Shortcomings in and criticisms of the theory *Origin of Species* related to Darwin's/Wallace's theory of natural selection and how those gaps were filled.

Introduction

This entry focuses on gaps in the initial theory of Charles Darwin in his 1859 book *On the Origin of Species by Means of Natural Selection or the Preservation of Favoured Races in the Struggle for Life* and its six subsequent revisions. This work can be summarized as two major arguments (Bowler 1989): First, it argued that species evolved via a process of “descent with

modification.” Second, it argued that this process was driven by natural selection, an evolutionary mechanism co-discovered with Alfred Russel Wallace that required a struggle for existence, variation with fitness consequences, and inheritance of that variation. This work remains standing as a centerpiece of current evolutionary thought. Despite this, acceptance of Darwin's work was never smooth sailing, as it faced a mix of criticism and praise from scientific and societal communities. Some bona fide gaps in the original theory were exposed by these critiques. Darwin was clearly moved by some of the criticism, as is evidenced in the book's revisions and in his correspondence with intellectual contemporaries. Other gaps existed but it is unclear whether Darwin recognized them.

By necessity, the coverage of gaps in this entry is somewhat selective but includes (a) arguably the most important gap in the lack of a proper understanding of genetics; (b) gaps of immediate relevance to researchers interested in the evolution of human behavior, including evolutionary psychology, in the theory's inability to explain seemingly maladaptive traits; and (c) gaps in the macroevolutionary claims in Darwin's early work which are of relevance for understanding the early theory's relevance for human evolution.

Fleeming Jenkin's Critique

In 1867, Scottish engineering professor, Fleeming Jenkin (Fig. 1), published a review of *Origin of Species* wherein he advanced a three-part critique



Gaps in Darwin's Initial Theory, Fig. 1 Fleeming Jenkin, a Scottish engineer, published a three-part critique of Darwin's initial theory. Darwin conceded to Jenkin with regard to the inheritance of variation but was unmoved by his criticism that the earth was insufficiently old. (Henry Charles Fleeming Jenkin. Etching by W. Holl, 1884. Credit: Wellcome Collection. CC BY)

of Darwin's ideas (Gayon 1998). The critique exposed two gaps in the initial theory and another that rested on reasonable-for-the-time theory that was later disproved.

The most famous of his criticisms centered on the inadequacy of blending inheritance, the mechanism favored by Darwin and his contemporaries, for sustaining natural selection (Charlesworth and Charlesworth 2009). Even when a trait confers a selective advantage, offspring fail to inherit it due to the "swamping effect" of blending. Rather, they will inherit a phenotype intermediate between their mother's and father's. Despite Jenkin's belief that this was problematic for the inheritance of small changes, but not large ones (referred to as "sports"), Darwin's theory rested on the accumulation of small changes. Darwin conceded to Jenkin in subsequent editions of *Origin of Species* and in a letter to Wallace. Jenkin's criticism lost its bite with the eventual acceptance of Mendel's

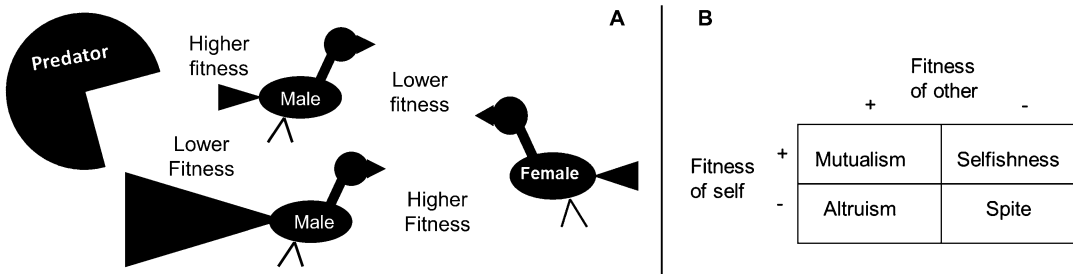
principles, which were published 2 years prior to the publication of Jenkin's review, but did not receive wide circulation until the turn of the twentieth century (Bowler 1989; Charlesworth and Charlesworth 2009; Gayon 1998). This paved the way for the "Modern Synthesis" – a new understanding of evolutionary processes and their consequences based on a tying together of Mendel's and Darwin's (and Wallace's) ideas.

Jenkin offered two additional points of criticism (Gayon 1998). The second was that variability within a species was bounded and that natural selection, thus, was insufficient to drive speciation. This is discussed in further detail below. The third criticism was that the earth was insufficiently old to have supported the evolution of its diverse life forms. This was a direct refutation of geologist Charles Lyell's findings, on which Darwin's theory was propped, that the earth was sufficiently old to have allowed "virtually unlimited amounts of time" (p.206) for evolution to have occurred (Bowler 1989). Jenkin's point here was based on a critique of Lyell's work by Lord Kelvin. Darwin was unconvinced by this part of Jenkin's criticism, which was for the best as Kelvin was proved wrong by advances in early twentieth century physics (Bowler 1989).

Explaining Seemingly Nonadaptive Traits

Darwin (1859) viewed his theory as providing a mechanism that would favor individually beneficial traits, never those that were "injurious to itself as natural selection acts solely by and for the good of each" (p.201). Explaining the existence, and thus evolution, of seemingly nonadaptive traits – such as aesthetic displays and altruism – was a gap in Darwin's initial theory (Fig. 2).

Darwin felt that his initial theory could not explain the evolution of exaggerated or purely ornamental features on the basis that they appeared nonadaptive (Bowler 1989; Cronin 1991; Jones and Ratterman 2009). In a letter written in 1860 to his friend, American botanist Asa Gray, he opined that "the sight of a feather in a peacock's tail, whenever I gaze at it, makes me sick!" Darwin presaged his eventual solution to the problem in *Origin of Species*, but it was in his second major work, *The Descent of Man, and*



Gaps in Darwin's Initial Theory, Fig. 2 Nonadaptive traits posed a problem for Darwin's initial theory: (a) extravagant displays, such as the peacock's train, were viewed as nonadaptive in the context of regular natural selection; as shown on the left, they might attract the attention of or slow the escape from predators. Darwin later elaborated the theory of sexual selection which can

favor these traits when they provide a mating benefit (as shown on the right). (b) Altruism, defined as behavior that benefits others at a cost to individual fitness, was a problem for Darwin's original theory that took a century to solve. There is a debate over whether Darwin himself recognized it as a problem

Selection in Relation to Sex (Darwin 1871), that he detailed the theory of sexual selection. In essence, he argued that it worked via two mechanisms: female choice (intersexual selection) and direct male-male competition (intrasexual selection). Darwin and Wallace disagreed about both mechanisms. Wallace argued that female choice could not have driven evolution and that traits that may have arisen via male-male competition, such as an elk's antlers, would evolve via regular natural selection for utilitarian purposes. Although Darwin was correct in essence, and there were some advances in the interim, sexual selection did not become part of the canon of evolutionary theory until the second half of the twentieth century (Cronin 1991).

Another problem with Darwin's initial theory was its inability to explain the evolution of altruism – those behaviors that provide a fitness benefit to others while incurring a cost to the actor (Cronin 1991; Dugatkin 2007; Ratnieks et al. 2011). Altruism includes, of course, traits such as alarm calling and providing care to young by parents and others. Darwin singled out the evolution of sterile workers in honeybees, something that today is viewed through the lens of altruism, as posing a “special problem” for his theory (Darwin 1859, p.236). While some see this as evidence that he puzzled over the evolution of altruism (e.g., Dugatkin 2007), others argue that he never recognized the problem as such (Cronin 1991; Ratnieks et al. 2011). Regardless, it was a

gap in the initial theory, and a satisfactory solution, despite being presaged by Darwin and others following him (Dugatkin 2007), was only offered with the formulation of inclusive fitness theory in the later half of the twentieth century. The delay in resolution, though certainly attributable to a multitude of factors, may have been caused to some degree by the debate over individual versus group selection (Domondon 2013; Ratnieks et al. 2011).

The Origin of Species and Transitional Forms

The lack of evidence for the second of Darwin's main claims, and the element of the theory from which derived the name of his most famous work – that natural selection would lead to the origin of new species – was an important problem for his theory. Huxley, for instance, who was otherwise one of Darwin's most vociferous allies (his “bulldog”), argued that the most conclusive evidence for selection would come when it can be shown to “produce a new species” (as quoted in Bowler 1989, p. 195). Darwin's erroneous ideas about what constituted a species have been pointed out as another weakness (Mallett 2008). Nonetheless, Darwin's ideas about the mechanisms that would drive speciation – geographic isolation – mirror modern ideas on allopatric speciation but downplay the ability of speciation to occur without it, which is today referred to as sympatric speciation.

Another related gap in the initial theory was the lack of “transitional forms” (Bowler 1989).

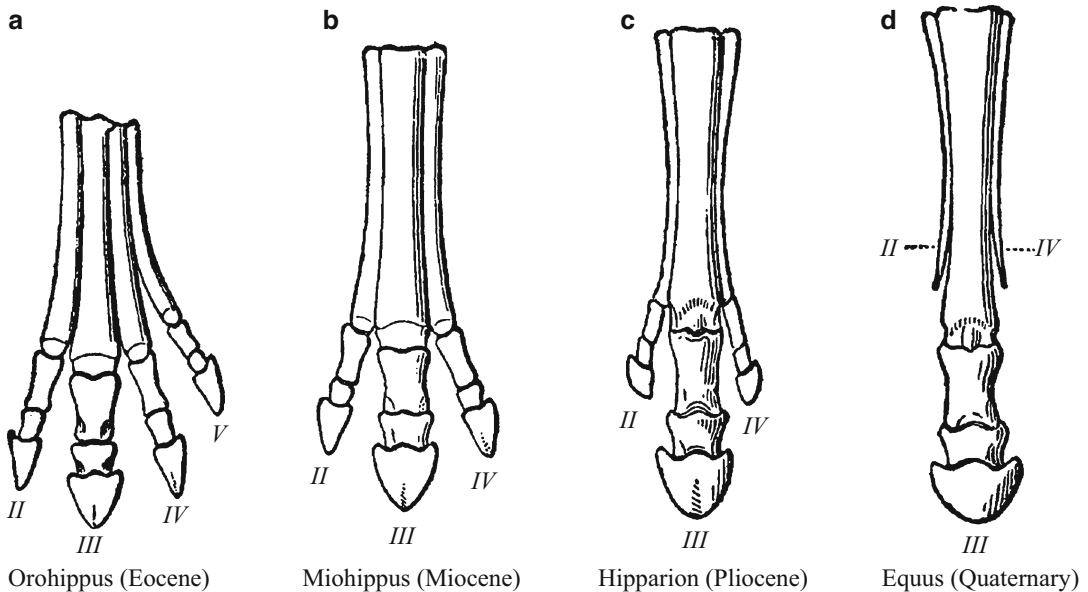
Darwin claimed in *Origin of Species* that fossils supported his theory but understood that there were weaknesses in the evidence. For instance, he argued at length that the gap-like nature of the record inevitably leads to the sudden appearance of species and the lack of transitional forms (Bowler 1989). Given this, he posed a strikingly indifferent stance on the appearance of clearly transitional forms found shortly after the first publication of *Origin of Species*. For instance, despite his close ally's gradual support for *Archaeopteryx* as transitional between reptiles and birds, Darwin included only one timidly phrased sentence about it in later revised editions. Gawne (2015) argues this may have been due to Darwin's position on species and his desire for more complete sequences (i.e., successions) rather than "missing links" such as those discovered later for early horses (Fig. 3), which Darwin called the "best support for the theory" (p.1082).

Finally, Darwin notably steered clear of applying his theory to human evolution in *Origin of Species* (Darwin 1859) but covered it in depth in his later writings, particularly *Descent of Man*,

and Selection in Relation to Sex (Darwin 1871). Part of the explanation was Darwin's worry that his ideas would be condemned on religious or moral grounds, but it was probably also due to the lack of the sorts of evidence for human evolution that we have today (Tattersall 2009). Neanderthals had been discovered a year before the publication of *Origin of Species*, and Darwin mentioned them in his later work. The more transitional, ape-like *Australopithecus* was not discovered until the first half of the twentieth century.

Conclusion

This entry focused on gaps in Darwin's initial theory – a theory he co-discovered with Wallace and then elaborated in his 1859 book. Rather than providing an exhaustive account of the perceived and real problems with the work that originated from the scientific community and from society at large, the entry has focused on a sample of gaps chosen for their relevance to evolutionary psychologists and others interested in the evolution



Gaps in Darwin's Initial Theory, Fig. 3 The lack of transitional forms was a gap in the evidence to support Darwin's initial theory. Later work, such as Othniel Marsh's fossil horses which showed a progressive

evolution toward a single toe, pictured here, was viewed as important evidence (Gawne 2015, p.1082). (Image: public domain)

of human behavior. In doing so, it should be clear that, although Darwin was fallible and not right about everything, he was a careful and thoughtful scholar, and the criticisms led to a refinement of his ideas where that was possible and necessary. This is in large part, along with its sheer simplistic elegance, why Darwin's early theory remains standing as a centerpiece of current evolutionary biological thought.

Cross-References

- ▶ [Alfred Russell Wallace and Charles Darwin](#)
- ▶ [Charles Darwin](#)
- ▶ [Charles Darwin: Theory of Sexual Selection](#)
- ▶ [History of Inheritance](#)
- ▶ [Impact of Early Theory on Charles Darwin](#)
- ▶ [Puzzle of Altruism, The](#)

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